

Palaeobiogeographic affinities of Upper Cretaceous ammonites of Northern Germany

By

HERBERT CHRISTIAN KLINGER & JOST WIEDMANN*)

With 16 text figures

KURZFASSUNG

Am verbliebenen Material von C. SCHLÜTER's Monographien „Beiträge zur Kenntnis der jüngsten Ammoniten Norddeutschlands“ (1867) und „Cephalopoden der oberen deutschen Kreide“ (1871-76) werden paläobiogeographische Beziehungen der deutschen Oberkreide-Ammonitenfauna aufgezeigt. Zahlenmäßig dominieren in der Fauna die Heteromorphen, besonders die Scaphiten und Vertreter der Nostoceratinae-Diplomoceratinae.

Das Auftreten von typischen „borealen“ Elementen, wie *Schloenbachia* und *Hyphoplites* während des Cenoman ist auffällig, sie werden begleitet von kosmopolitischen Faunen, besonders Turrilitinae. Während der übrigen Oberkreide ist die deutsche Fauna nicht so sehr durch das Auftreten von typischen „borealen“ Elementen gekennzeichnet, sondern eher

durch das Fehlen oder die Seltenheit von anderen weit verbreiteten Faunenelementen, wie den Tetragnitidae, Texanitinae, Barroisiceratinae, Kossmaticeratinae und Gaudryceratinae. Die engen Beziehungen zwischen der Fauna des alpinen Gosaubeckens mit Südafrika ist rätselhaft.

Es scheint, daß die sogenannte weltweite Verbreitung von einigen Faunen auf Fehlinterpretationen beruht; wir hoffen, dies demnächst mit einer ausstehenden Revision beweisen zu können. Hierher gehören unter anderem die Arten *Anapachydiscus wittekindi*, *Gauthiericeras margae*, *Baculites leopoliensis* etc. Gegen Ende der Kreide erscheinen bei einigen Baculiten und Scaphiten Einschränkungen in der geographischen Breite.

ABSTRACT

On the basis of a revision of the remaining figured material of CLEMENS SCHLÜTER's classical monographs "Beitrag zur Kenntnis der jüngsten Ammoniten Norddeutschlands" (1867) and "Cephalopoden der oberen deutschen Kreide" (1871-76), an attempt is made to determine the palaeobiogeographic affinities of the Upper Cretaceous German ammonite fauna. Inherent errors in interpreting palaeobiogeographic data are pointed out.

In terms of numbers of species, the fauna is dominated by the heteromorphs; especially the scaphitids and Nostoceratinae-Diplomoceratinae.

During the Cenomanian Stage the presence of typical "Boreal" faunas such as *Schloenbachia* and *Hyphoplites* is conspicuous, accompanied by widely cosmopolitan faunas, especially Turrilitinae. During the remainder of the Cretaceous

the German faunas are characterized not so much by the presence of typical "Boreal" faunas, but rather by the absence or paucity of other widely distributed faunas. These include the Tetragnitidae, Texanitinae, Barroisiceratinae, Kossmaticeratinae and Gaudryceratinae. Furthermore, the close relationship between the nearby Gosau Basin of Austria with southern Africa is an enigma.

It appears that the so-called world wide distribution of some faunas may be due to misinterpretation; a short-coming we hope to rectify with the pending revision. Species include, amongst others, *Anapachydiscus wittekindi*, *Gauthiericeras margae*, *Baculites leopoliensis* etc. Towards the end of the Cretaceous, latitudinal restriction seems to occur amongst some baculitids and scaphitids.

*) H. C. KLINGER, South African Museum, P. O. Box 61, Cape Town 8000, South Africa; J. WIEDMANN, Institut und Museum

für Geologie und Paläontologie der Universität, Sigwartstr. 10, D-7400 Tübingen.

ACKNOWLEDGEMENTS

Thanks are due to Professor Dr. H. REMY (Bonn) and Dr. S. RITZKOWSKI (Göttingen) for access to their collections, and to the ALEXANDER VON HUMBOLDT-Stiftung for financial support during

H. KLINGER's stay in Tübingen, and also for covering the cost of printing of this article. Further thanks are due to the C.S.I.R. and Board of Trustees of the South African Museum for financing his visit to Munich. Financial support by D.F.G. of J. WIEDMANN's visit of South African Cretaceous is appreciated.

CONTENTS

Introduction 414
Faunal Composition 416
Faunal Distribution through Time 416
Summary 424
List of References 425

INTRODUCTION

More than a century ago CLEMENS SCHLÜTER described the cephalopoda of the Upper Cretaceous deposits of Germany in his two classical works: "Beitrag zur Kenntnis der jüngsten Ammoneen Norddeutschlands" (1867) and "Cephalopoden der oberen deutschen Kreide" (1871-76). Up to the present day, SCHLÜTER's work remains the standard source of reference for ammonite research in West and Central Europe, and even farther afield. In addition, important parts of the stratigraphic zonation in Europe were based on SCHLÜTER's work (cf. HANCOCK & KENNEDY 1981).

Apart from the fact that names and concepts in the field of ammonite systematics have changed considerably over the past century, SCHLÜTER's figures are all lithographs. Bearing in mind the notoriety of some 19th century artists as far as incor-

rect, and misleading restorations are concerned, a revision based on examination of the type material is long due. Ideally, this revision should also include material collected under strict stratigraphic control, but, as WIEDMANN (1979) has pointed out and from personal experience, many of the original localities are no longer accessible. Nevertheless, this has been undertaken on modest scale by GIER (1964), HANCOCK et al. (1972), LOMMERZHEIM (1976), SCHMID & ERNST (1975), WIEDMANN & SCHNEIDER (1979), KAPLAN et al. (in press).

With this pending revision in view, we managed to trace 85% of the figured material of SCHLÜTER's 1867 publication, and slightly more than half of his later (1871-76) work. Hopefully photographic illustration and redescription of this material will help towards clearing a number of stratigraphic and

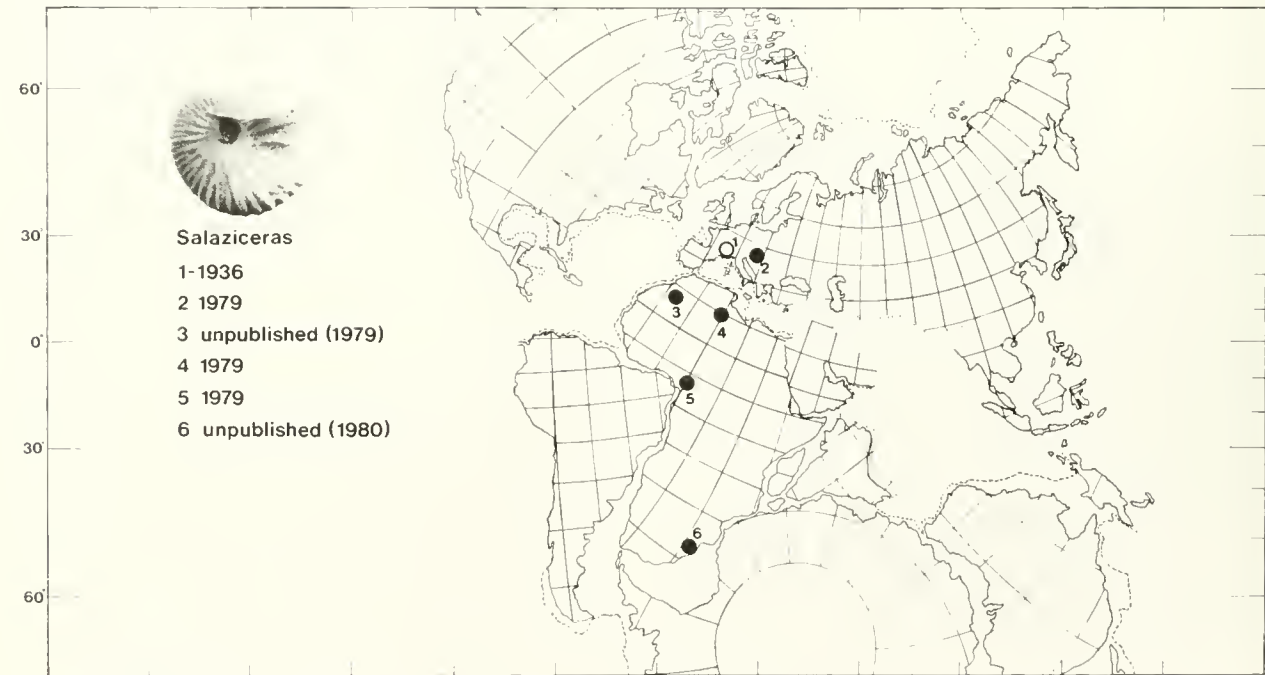


Fig. 1. Map showing change in distribution of the alleged "endemic" genus *Salaziceras* BREISTROFFER through insufficient data. (Palaeogeographic reconstructions refers in this and the following figures to about 135 MYA, i. e. the Jurassic-Cretaceous boundary.)



Fig. 2. Map showing change in distribution of genera *Colchidites* DJANELIDZE and *Heteroceras* D'ORBIGNY from virtually Tethyan ten years ago to cosmopolitan by recent data.



Fig. 3. Recent *Nautilus* found in nature reserve Cape of Good Hope, South Africa. Coll. South African Museum. Nat. size.

systematic "potential headaches" as tactfully phrased by HANCOCK & KENNEDY (1981: 543).

Arising from this revision, we have attempted to determine the palaeobiogeographical affinities (if any at all!) of the Upper Cretaceous ammonites from northern Germany. Basically this is a mere extension of WIEDMANN'S (1979) correlation of the ammonite faunas of northern Germany, Regensburg, East Alpine and the western Mediterranean; more specifically northern Spain and Morocco. Here we extend comparisons to include the Malagassy and southern African successions, as recent observations on the Gosau Cretaceous have shown strong links with this Gondwana fauna (SUMMESBERGER 1979; IMMEL et al. 1982). Relevant parts of the Indopacific region are also included.

These observations overlap to a great extent with those of MATSUMOTO (1973), COLLIGNON (1977) and HANCOCK & KEN-

NEDY (1981), hence we concentrate to a greater extent on the faunal affinities, rather than strict stratigraphic correlation.

Factors influencing the interpretation of palaeobiogeographic data were recently summarized by KENNEDY & COBBAN (1976) (see also KENNEDY & JUIGNET 1976). To illustrate the thin ice on which we are treading, the distribution of the taxa *Salaziceras* BREISTOFFER (Fig. 1) and *Heteroceras* D'ORBIGNY and *Colchidites* DJANELIDZE (Fig. 2) is illustrated on the basis of data collected over the last ten years as well as recent *Nautilus*. The distribution of *Salaziceras* has changed from endemic to virtually pandemic; *Colchidites* and *Heteroceras* have changed from latitudinally restricted, typical tethyan taxa to cosmopolitan (barring the typical European Boreal Realm), and *Nautilus* is now known from the Cape of Good Hope (Fig. 3).

FAUNAL COMPOSITION

In terms of numbers of species, we see that the fauna is dominated by heteromorphs; especially the scaphitids and the Nostoceratinae-Diplomoceratinae plexus, followed by the Turrilitinae, Baculitinae and Anisoceratinae. Amongst the "normally"-coiled ammonites, the Pachydiscidae, Collignon-

iceratidae and Acanthoceratidae are dominant, with really insignificant proportions of Phylloceratidae, Tetragonitidae, Gaudryceratidae and Puzosiinae – the latter in terms of relative abundance as well.

FAUNAL DISTRIBUTION THROUGH TIME

A. CENOMANIAN (Fig. 4, 5)

The Cenomanian is characterized by transgressions in many parts of the world. Lowermost Cenomanian faunas of this transgression were recently described by WIEDMANN & SCHNEIDER (1979) from Mülheim-Broich. These include *Utaturiceras vicinale*, a species hitherto only recorded from the Cenomanian of India and Madagascar (but probably also present in Zululand), thereby again illustrating how lack of data can slant palaeobiogeographical interpretation.

A characteristic of the German Cenomanian is the presence of typical "Boreal" and cosmopolitan faunas. The Albian Hoplitinid or European Province (OWEN 1971, 1973) is still present; the dominant genera now being *Schloenbachia* and *Hyphoplites*. Where these occur, they are the dominant elements of the ammonoid fauna. Co-occurring with these "Boreal", restricted faunas, are true cosmopolitan forms, of which especially the Turrilitinae (Fig. 5) are conspicuous, including species *Turrilites costatus*, *T. acutus*, *T. scheuchzerianus*, *Neostlingoceras carcitense*, *Hypoturrilites gravesianus*, *H. tuberculatus*, *Mariella* spp. etc. Other heteromorph cosmopolitan forms include *Sciponoceras baculoide*, *Scaphites* spp., *Idihamites* spp. and *Anisoceras* spp. Amongst the Acanthoceratidae many cosmopolitan species also occur, in-

cluding *Metoicoceras geslinianum*, *Acompsoceras sarthense*, *Mantelliceras mantelli* etc. All these allow for worldwide correlation during the Cenomanian (Fig. 4).

Conspicuous absentees from the European Boreal are the Tetragonitidae, which seem to follow the Tethyan/Boreal border very closely in Europe (WIEDMANN 1973); a trend which is to continue with few exceptions throughout the Cretaceous. The acanthoceratid *Graysonites* has not yet been recorded from Boreal Europe, but this may be due to non-exposure. It is known from Spain (WIEDMANN 1978, 1980).

The boundaries between the European Boreal Realm and the Tethys are perfect examples of filter routes. What we do not know is what the element is which is responsible for this selective distribution. The most common cause cited is temperature, but this has been disproved (see KENNEDY & COBBAN 1976 for summary); instead HALLAM'S (1969, 1972) fluctuating environment model appears closer to the truth. WIEDMANN et al. (1978, 1980) ascribe the presence of Boreal faunas in Morocco due to upwelling.

This division between European Boreal and cosmopolitan or non-Boreal faunas is to continue throughout the Cretaceous with differing degree. What does emerge from the distributional pattern is that this barrier cuts across systematic and morphological boundaries.

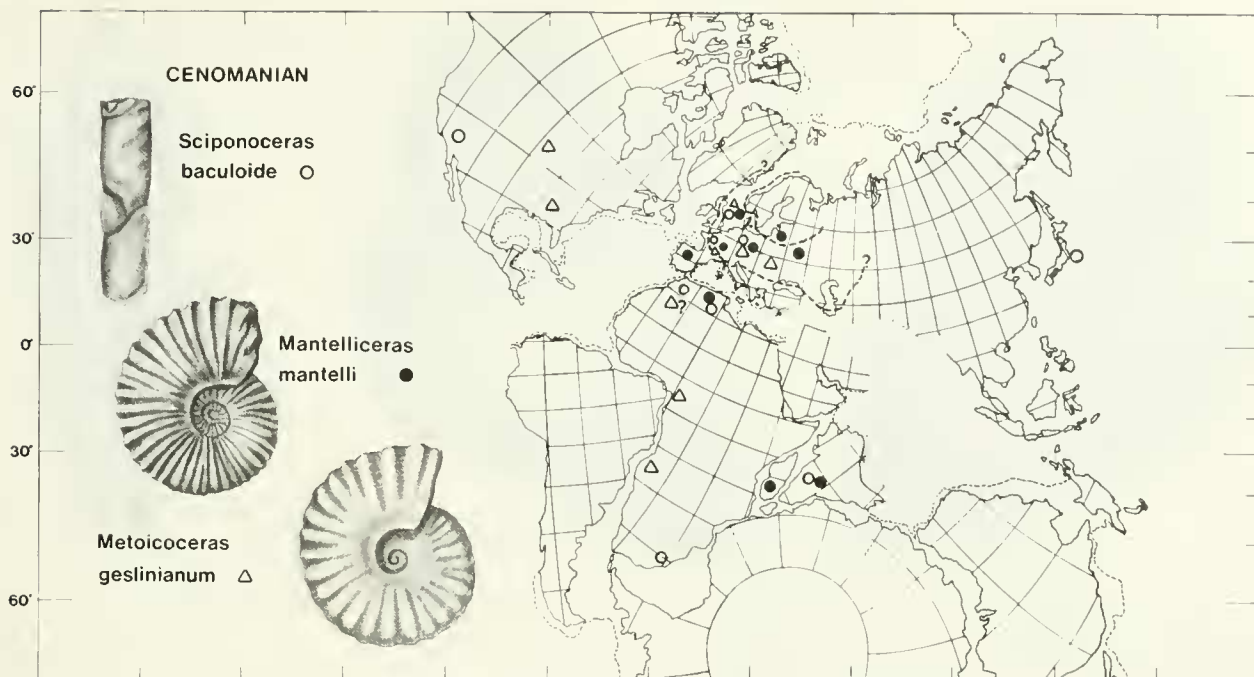


Fig. 4. Map showing cosmopolitan distribution of some taxa in the Cenomanian, and the outline of the Albian "Hoplitinid" Realm.

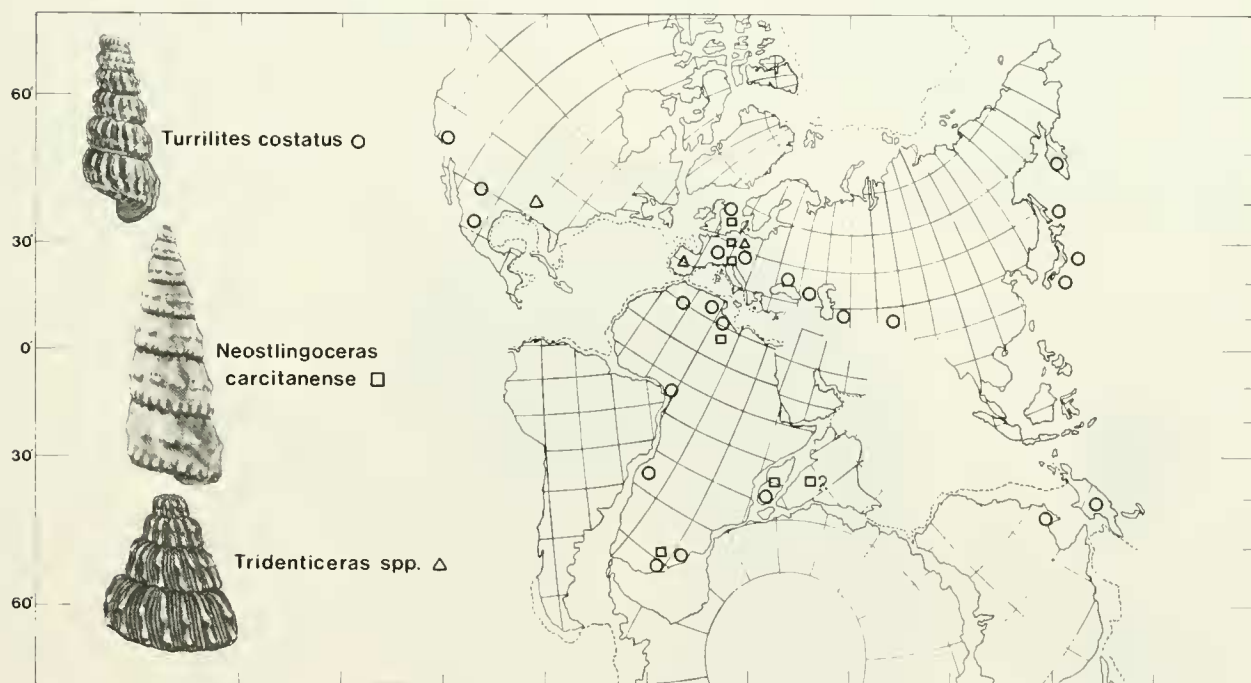


Fig. 5. Map showing cosmopolitan distribution of Cenomanian turrilitids *Turrilites costatus* and *Neostlingoceras carcitanense* in contrast to disjunct distribution of the Coniacian turrilitid genus *Tridenticeras*, illustrating that shell morphology in this case seems to have little influence on distributional pattern.



Fig. 6. Photograph of original of *Turritiles cenomanensis* SCHLÜTER to illustrate idealized reconstruction. Nat. size.

B. TURONIAN (Fig. 7)

The Turonian ammonites of northern Germany differ in their affinities from group to group. Unlike their Cenomanian counterparts, the heteromorphs show peak endemism, and in addition, seem to be facies controlled. These include *Otoscapites bladenensis*, *Scaphites geinitzi* s. l., *Hyphantoceras reussianum*, *Pseudoxylloceras* (*Christophoceras*) *multinodosum*, *Allocrioceras angustum*, *A. strangulatum*; all mainly known from the Turonian of Germany and England (see WRIGHT 1979). An exception seems to be the baculitid *Sciponoceras bohemicum* which has been tentatively reported

from Japan and California. Much of this apparent endemism may possibly be due to inconsistent systematic procedure, resulting from extreme intraspecific variation. Similarly, some species have been interpreted too widely. Thus reports of *Hyphantoceras reussianum* from the Lower Campanian of Madagascar are certainly based on misidentification.

Peak endemism amongst heteromorphs is recorded from Japan, and correlation with Europe on the basis of these is impossible at specific level. In contrast, Madagascar, which has gained virtual notoriety for its diverse heteromorph fauna during all the other stages of the Cretaceous is now characterized by the virtual absence of these. In southern Africa no onshore Turonian sediments have yet been found.

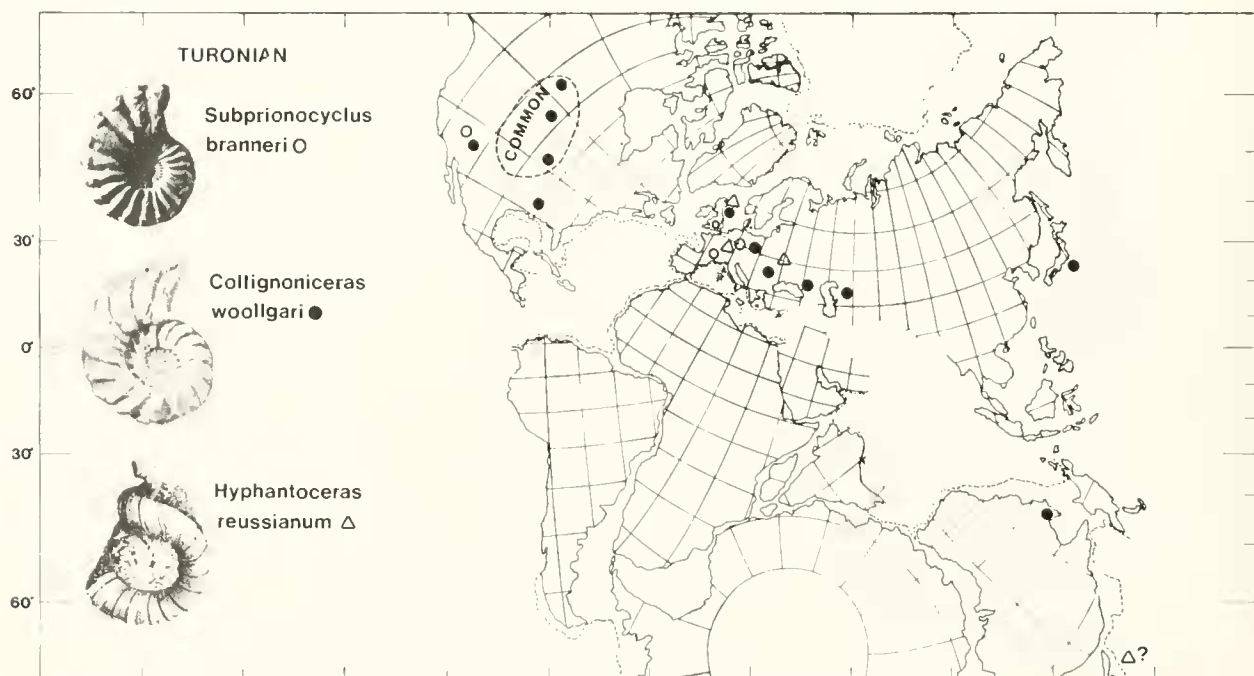


Fig. 7. Map showing distribution of select taxa during the Turonian.

In contrast, some representatives of the subfamily Collignoniceratidae are virtually cosmopolitan; especially in the genus *Subprionocyclus*. In the Upper Turonian these include *S. neptuni*, *S. branneri* and *S. normalis*. In the Middle Turonian *Collignoniceras woollgari* has wide distribution. *Le-*

cointriceras fleuriausianum from the Zone of *Collignoniceras woollgari* is known from Germany, France, England and Spain. Amongst the Acanthoceratids, *Mammites nodosoides* from the Lower Turonian is another cosmopolitan species.

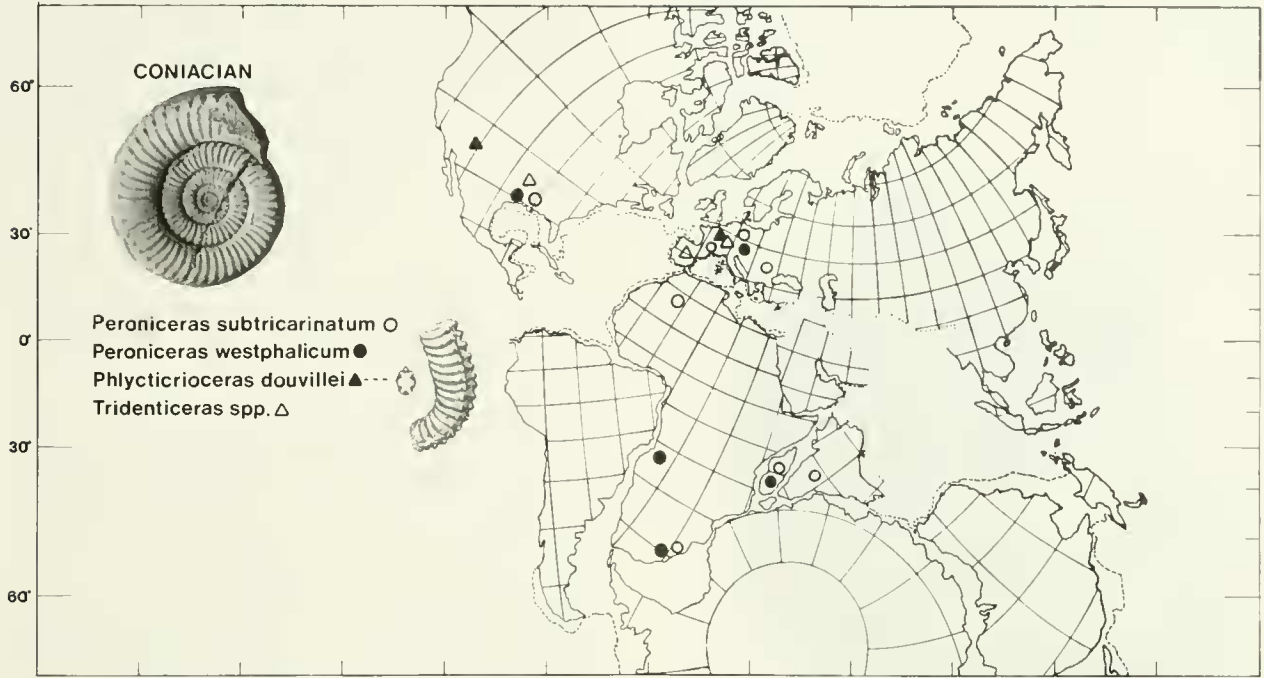


Fig. 8. Map showing cosmopolitan distribution of the representatives of the subfamily Peroniceratinae and disjunct distribution of *Phlycticrioceras douvillei* (DE GROSSOUVRE), Coniacian.



Fig. 9. Holotype of *Gauthiericeras margae* (SCHLÜTER), housed in the collections of the Geologisch-Paläontologisches Institut, Bonn. Reduced.

C. CONIACIAN
(Fig. 8)

During the Coniacian we again have perfect correlation at specific level in the family Collignoniceratidae; more specific the subfamily Peroniceratinae, between northern Germany, Africa, Madagascar, and to a lesser extent the Indo-pacific region. Species which can be traced worldwide include *Peroniceras subtricarinatum*, *P. tridorsatum*, and *P. westphalicum*



Fig. 10. Photograph of the specimen of *Peroniceras westphalicum* (STROMBECK) figured in dorsal view by SCHLÜTER (1867, pl. 6, fig. 2). Reduced.

(Fig. 10). Characteristic of the fauna is its paucity in N. Germany – a trend which is to continue in the European “Boreal” to the eventual exclusion of the Collignoniceratidae from this region. Even though the Peroniceratinae seem to have originated in the European part of the Tethys, they reach their maximum development in the Coniacian of Zululand, evolving into smooth, unicarinate oxycones.

Inconsistent interpretation of *Gauthiericeras margae* (Fig. 9) may be responsible for the differing stratigraphic placing of the species in various parts of the world. In Germany, Spain and north Africa, the species is placed in the Middle Coniacian, whereas in Madagascar (where it is the zonal index) and Zululand, it is reported from the Upper Coniacian. At the Craie de Villedieu, *G. margae* has been found near the base of the section (HANCOCK & KENNEDY 1981). Present revision (KLINGER & KENNEDY in prep.) seems to indicate that the Afro-Malagassy forms may belong to a species different to that of Europe.

Amongst the subfamily Texanitinae, a doubtful record of *Paratexanites emscheris* connects Zululand with north Germany. A notable absentee is the genus *Protexanites*. However, wherever the genus occurs, it is sparsely represented in numbers (KLINGER & KENNEDY 1980), and its absence in Germany may be due to collecting failure.

Also amongst the Collignoniceratidae, the absence of the subfamily Barroisiceratinae, with the exception of *Harleites alstadenensis*, more specific the genera *Forresteria*, *Reesidites* and *Yabeiceras*, some of which are locally common in Zululand, Madagascar, Japan and southern U.S.A. is conspicuous.

Also notably absent are the families Tetragonitidae, Kossmaticeratidae, Gaudryceratidae – as will also be noted up to the end of the Cretaceous.

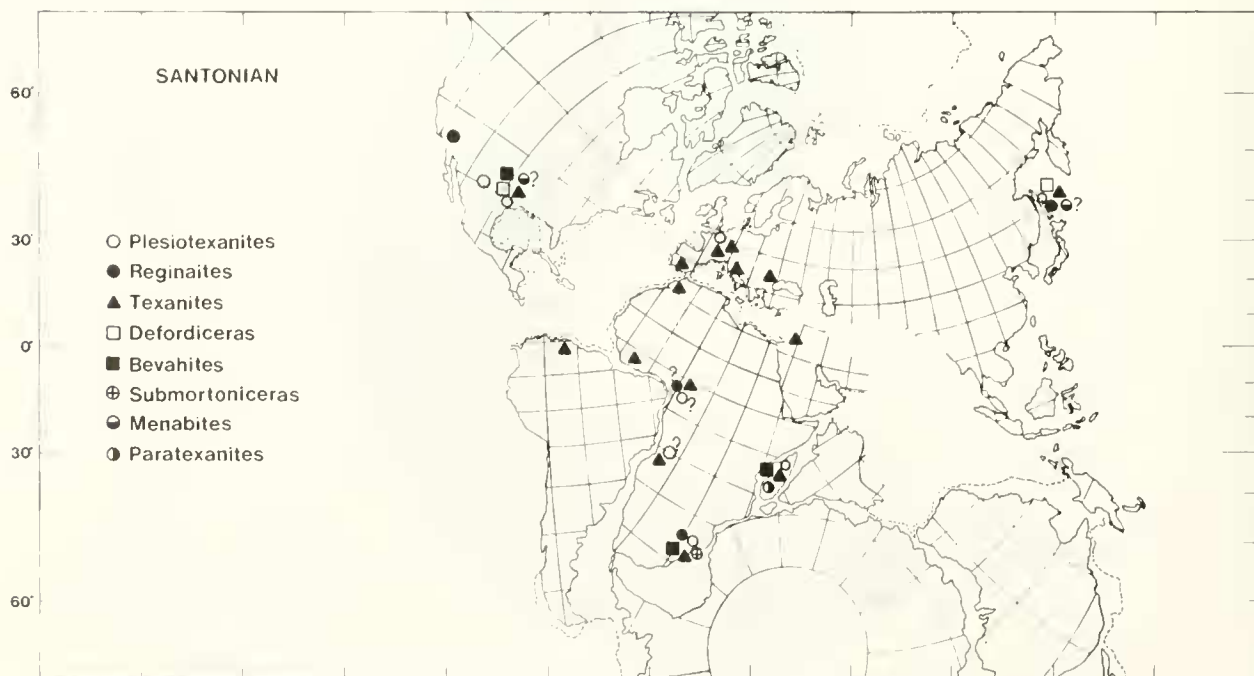


Fig. 11. Map showing wide distribution of the ammonite subfamily Texanitinae COLLIGNON during the Santonian, including northern Germany.

Amongst the heteromorphs, *Tridenticeras* can be compared at generic level with northern Spain and Texas, whereas *Phlycticrioceras douvillei* is known from the Coniacian of Germany, France, Oregon and New Mexico.

Thus, during the Coniacian only some Peroniceratinae in the German Cretaceous have cosmopolitan affinities. The absence of Tetragonitidae, Gaudryceratidae, Kossmaticeratidae, most Barroisiceratinae is characteristic of the European "Boreal" during the Coniacian.

D. SANTONIAN

(Fig. 11)

During the Santonian the dissimilarities rather than similarities between the European Boreal, and non-Boreal faunas become conspicuous. In contrast to southern Africa, Madagascar, the Gulf and Pacific Coasts of the U.S.A., Japan and the Tethyan part of Europe, the subfamily Texanitinae is a rarity in northern Germany, being represented by a single specimen of *Plesiotechanites schlueteri*, two of *Paratexanites rex* and an uncertain number of *Texanites pseudotexanum*. In Zululand and Pondoland texanitids occur by the hundreds (KLINGER & KENNEDY 1980); in Madagascar (COLLIGNON 1977) has collected 800 specimens of *Texanites*.

Another conspicuous absentee in the Boreal part of Europe is the genus *Pseudoschloenbachia*, apart from the already predictable tetragonitids, gaudryceratids, and kossmaticeratids.

Stantonoceras depressum is common to northern Germany and France whereas *Placentoceras syrtale* is common to northern Germany and the Gosau. At generic level these species show similarities to forms from the southern U.S.A.

At this stratigraphic level, the contrasting affinities of the East Alpine Gosau, and the north German Cretaceous are striking. In direct contrast to the Boreal north German Cretaceous the Gosau shows distinct afro-malagassy affinities (WIEDMANN 1978; SUMMESBERGER 1979; IMMEI et al. 1982). The Gosau contains species such as *Texanites quinquenodosus*, *Paratexanites serratomarginatus*, *Reginaites gappi*, *Hauericeras gardeni*, *Hyphantoceras* (*Madagascarites* ?) *amapondensis*, *Kitchinites stenomphalus*, *Skoumalia austriaca*, *Neocrioceras* (*Schlueterella*) *compressum*, *Anagaudryceras* cf. *subtilineatum*, *Saghalinites* aff. *wrighti*, *Pseudophyllites latus*, *Damesites* cf. *compactus*, *Kossmaticeras* cf. *sparsicostum*, *Eulophoceras natalense*, *Diplomoceras* (*Glyptoxoceras*) *subcompressum*, all of which occur, or have closely related counterparts in the Santonian of Madagascar, Zululand and Pondoland. Close comparisons also exist between the Santonian of the Gosau and India, but surprisingly, no texanitids have as yet been recorded from India (COLLIGNON 1948; SASTRY et al. 1968; HANCOCK & KENNEDY 1981) – nor for that matter from Australia or New Zealand. An as yet undescribed texanitid fauna is known from Patagonia (KATZ 1963).

Euhomaloceras incurvatum, known from northern Germany, W. Europe and the Gosau may possibly be a senior synonym of *Baculites capensis*, in which case the distribution may be expanded to include the Santonian of Pondoland, Zululand, Madagascar, Japan and California.

All in all, the north German ammonite faunas are typically Boreal, and are characterized not so much by the presence of certain taxa, but rather by their absence or poor representation. This of course, causes severe difficulty in global correlation (see HANCOCK & KENNEDY 1981).

E. CAMPANIAN

(Fig. 12, 13, 14)

Affinities of the Campanian ammonoid fauna of northern Germany are virtually a continuation of the trend initiated in the Coniacian, and firmly established in the Santonian. No texanitids at all are known from northern Germany. In other areas where the subfamily Texanitinae does occur, the genera *Menabites* s. l., *Bevabites* and *Submortoniceras* are typical of the Lower and Middle Campanian (Fig. 12).

The family Tetragonitidae is represented by one species, *Tetragonites obscurus*. The absence of the ubiquitous genus *Pseudophyllites* is striking, considering the virtual cosmopolitan distribution of the genus (KENNEDY & COBBAN 1976).

Most of the scaphitids appear latitudinally restricted or endemic, but some are good for correlation between Europe and North America. *Scaphites hippocrepis*, which marks the base of the Campanian (COBBAN 1969) occurs all over Europe, and in the Western Interior, Gulf and Atlantic Coastal Plains of North America. *Trachyscaphites spiniger* has the same geographical distribution, and marks the Lower Upper Campanian. Neither of these is found in the southern Hemisphere (Fig. 13). In addition, several scaphitid genera appear restricted to the northern hemisphere, or endemic, e. g. *Acanthoscaphites*, *Clioscapites*, *Desmoscapites*, *Discoscaphites*, *Haresiceras*, whereas *Hoploscapites* appears cosmopolitan.

Nearly all the "normal" pachydiscids recorded from northern Germany seem confined to Europe and European USSR. In addition, the family as a whole seems to be in need of restudy. Records of *Anapachydiscus wittekindi* from the Lower Campanian of Madagascar (COLLIGNON 1960, 1969) and the second division of the Campanian from Zululand (KENNEDY & KLINGER 1975) are either based on misidentifications, or the species has a very long range; being known from the Upper Campanian Zone of *Bostrychoceras polyplocum* in Europe.

Surprisingly the micromorphic pachydiscids, e. g. *Patagiosites*, *Urakawites*, *Mennites* and *Pseudomennites* have a world-wide distribution at generic level, but are always poorly represented in terms of numbers.

Even though details of species still have to be worked out, the Upper Campanian is marked by the presence of the cosmopolitan genus *Hoplitolacentoceras* (Fig. 14) (even though it ranges locally into the Lower Maastrichtian in France [HOWARTH 1960: 391]).

The phylloceratid *Partchiceras forbesianum* (= SCHLUTER's *Ammonites velledaeformis*, pl. 18, fig. 6 only) occurs nearly world-wide in the Campanian, having been recorded from Europe, Japan, New Zealand, British Columbia, Alaska, Madagascar, Graham Land and Siberia – this distribution pattern is in stark contrast to the restricted occurrence of *Phylloceras velledaeformis* – known only from Germany and Denmark.

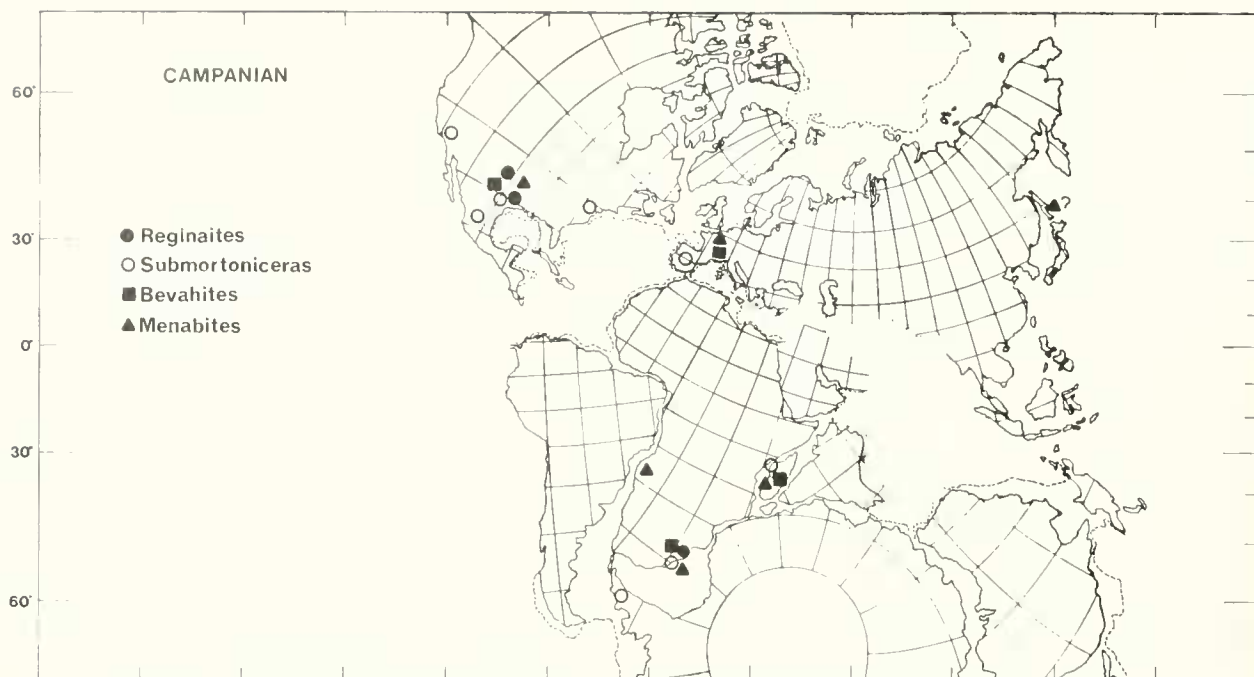


Fig. 12. Map showing restricted distribution of ammonite subfamily Texanitinae COLLIGNON during the Campanian.

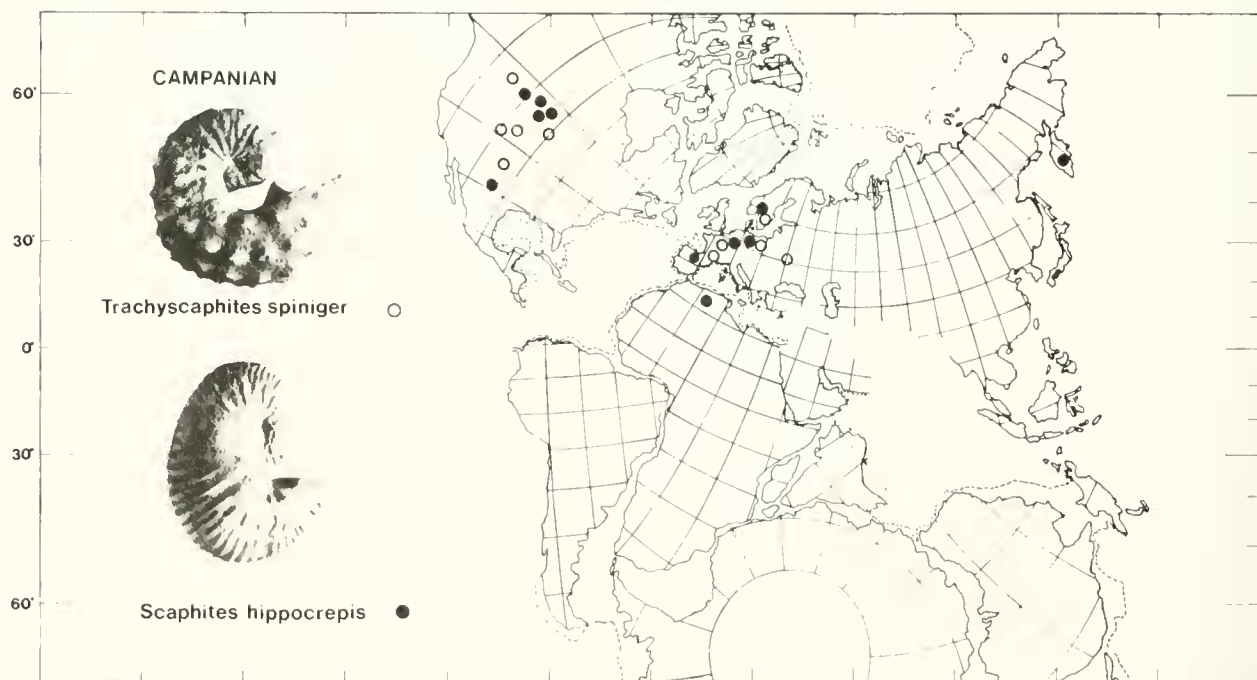


Fig. 13. Map showing apparent latitudinally restricted distribution of some scaphitids during the Campanian.

Even though SCHLÜTER described a large number of heteromorphs from the Campanian, no typical Nostoceratids, such as are known from U.S.A., Angola, Madagascar or Israel seem present in Boreal Europe. Instead, *Bostrychoceras polyplacum* occurs in great numbers in the Upper Campanian. Many of the Campanian heteromorphs have a wide distribution in Europe, e. g. *Neocrioceras* (*Schlueterella*) *pseudarmatum*, *Pseudoxybeloceras* (*Parasolenoceras*) *interruptus*,

Glyptoxoceras retrorsum, "*Neancyloceras*" *bipunctatum* etc., but at generic level occur world-wide.

Records of Boreal European baculitids from other areas have to be viewed with caution. Thus the tentative record of *B. anceps* from California has been referred to *B. subanceps pacificus*, a northern Hemisphere subspecies of the Upper Campanian Angolan *B. subanceps subanceps* (HOWARTH 1960). COLLIGNON (1969) used *Baculites leopoliensis* as an in-

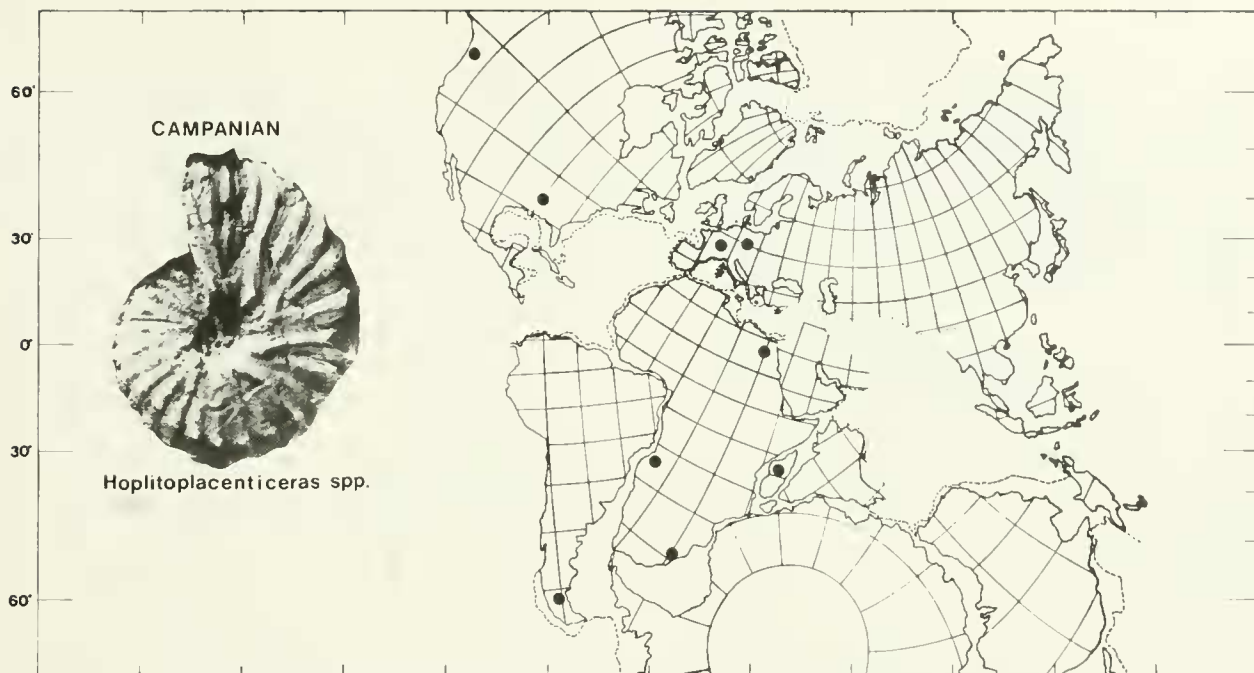


Fig. 14. Map showing cosmopolitan distribution of genus *Hoplitoplacenticeras* during the Campanian.

dex for the Middle Campanian of Madagascar, but in North Germany, Poland, European USSR and Central Asia it occurs in the Upper Campanian Zone of *Bostrychoceras polyplacum* (cf. ATABEKIAN & KHAKIMOV 1976). Again we have to question this identification.

F. MAASTRICHTIAN (Fig. 15, 16)

Pachydiscus neubergicus is usually taken to mark the Lower Maastrichtian and has a wide distribution (Fig. 15). Unfortu-

nately, however, doubt now exists if this species is really restricted to the Lower Maastrichtian (BIRKELUND 1979) or conversely, if juvenile pachydiscids can be satisfactorily identified (HANCOCK & KENNEDY 1981).

The characteristic faunal element of the Lower Maastrichtian in the southern Hemisphere is the genus *Eubaculites*. This consists of about four species with overlapping morphologies and stratigraphic ranges (KLINGER 1976), but has been recorded in reasonable numbers from southern India, West Australia, New Zealand, Madagascar, Mozambique, Zululand, offshore southern Cape, Peru, Chile and Argentina (Fig. 16).

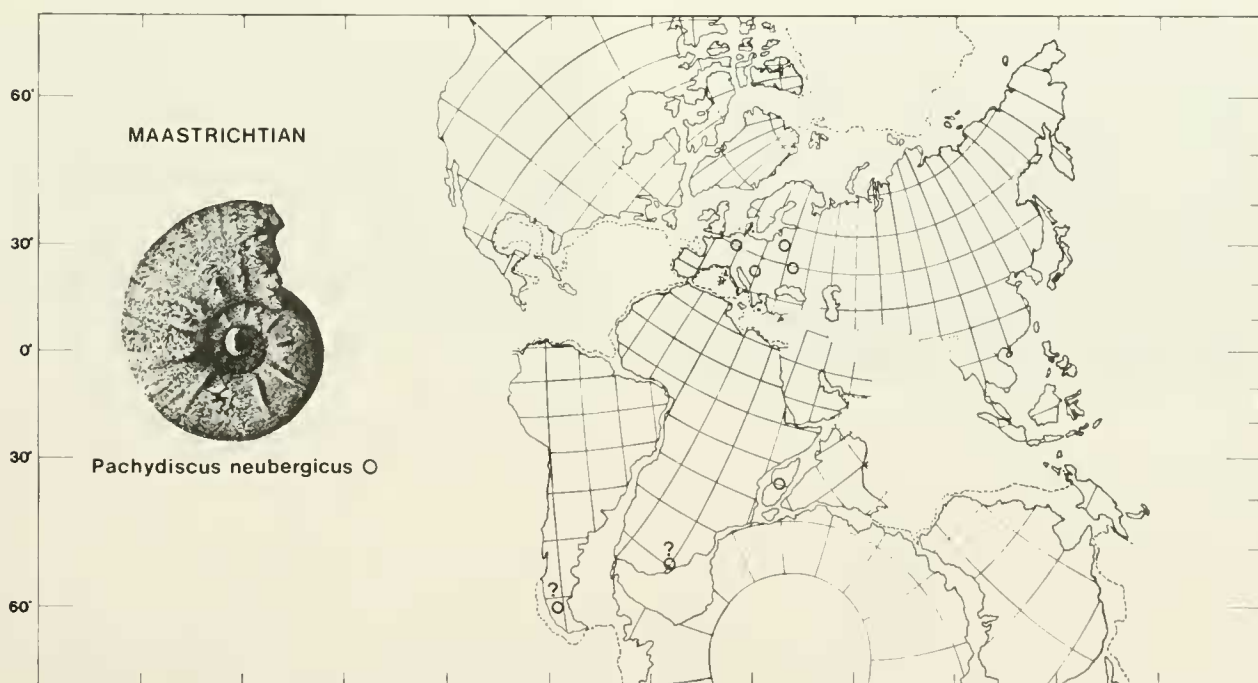


Fig. 15. Map showing distribution of doubtful records of *Pachydiscus neubergicus*.

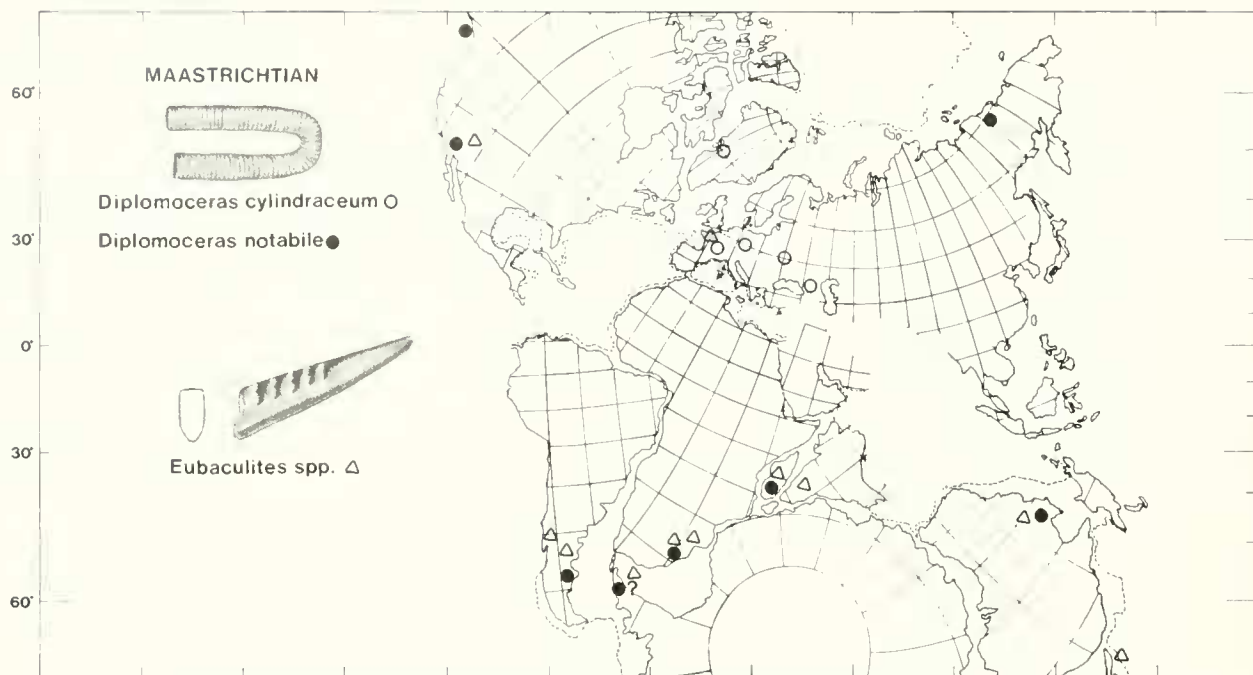


Fig. 16. Map showing latitudinally restricted distribution of *Eubaculites* spp. and apparent Boreal and non-Boreal distribution of *Diplomoceras cylindraceum* (DEFRANCE) and *D. notabile* (WHITEAVES).

Only a few specimens are known from California (MATSU-MOTO 1959) and a single figured specimen from Limbourg (BINCKHORST 1861). KENNEDY (pers. comm.) also recorded it from Neuberg in Austria. This appears to be one of the few taxa with potential for world-wide correlation, even though its major occurrence is distinctly austral.

Diplomoceras cylindraceum has been widely cited from the Lower Maastrichtian of Europe, European USSR and Cri-

mea, whereas the non-Boreal counterpart, *D. notabile* is widely recorded elsewhere. Unfortunately, however, these species, if interpreted correctly, seem to have long stratigraphic ranges. BIRKELUND (1979) records *D. cylindraceum* for the whole of the Maastrichtian, whereas *D. notabile* already seems to occur in the Upper Campanian of Zululand (Fig. 16).

SUMMARY

During the Cenomanian distinct European Boreal genera exist, which clearly define the borders of this Realm, but they are accompanied by cosmopolitan forms. Subsequently, no typical European Boreal genera occur, but we do seem to have latitudinal restriction amongst the baculitids and scaphitids towards the end of the Cretaceous. In addition, the European Boreal Realm is characterized not so much by the presence of certain faunas, but rather by their absence or paucity. These include the families and subfamilies Texanitinae, Tetragonitidae, Gaudryceratidae, Kosmaticeratidae, Barroisiceratidae, and Pseudoschloenbachinae. These groups occur at virtually

all latitudes outside it so that temperature as a controlling factor can be ruled out, as already shown by WIEDMANN (1973).

It appears that most attempts at interpretation of palaeobiogeographical data lead to more questions than answers. Examples here are the absence of Texanitinae and Pseudoschloenbachinae from Australia and New Zealand.

On the basis of the ammonite distribution here presented, there seems to be no need for separation of a distinct Austral Realm as suggested, amongst others, by STEVENS (1973).

REFERENCES

- ATABEKIAN, A. A. & KHAKIMOV, F. K. (1976): "Campanian and Maastrichtian ammonites of Central Asia" (In Russian). – Akad. Nauk. Tadzhik SSR, 1976: 1–146.
- BINKHORST, J. T. (1861): Monographie des gastéropodes et des céphalopodes de la craie supérieur du Limbourg. Brussels.
- BIRKELUND, T. (1979): The last Maastrichtian ammonites. – In: BIRKELUND, T. & BROMLEY, R. G. (Eds.) Cretaceous-Tertiary boundary events, 1, The Maastrichtian and Danian of Denmark, 51–57.
- COLLIGNON, M. (1948): Ammonites néocétacés du Menabe (Madagascar). 1. Les Texanitidae. – Ann. géol. Serv. Mines Madagascar, 13: 47–107; 14: 1–101.
- (1969): Atlas des fossiles caractéristiques de Madagascar. (Ammonites) 15 (Campanien Inférieur). – Service Géologique: Tananarive.
- (1977): Essai de comparaison des faunes d'ammonites au Crétacé supérieur (Turonien à Maastrichtien) au Japon et à Madagascar. – In: MATSUMOTO, T., (Ed.) Mid-Cretaceous Events, Hokkaido Symposium 1976. – Palaeont. Soc. Japan, Spec. Pap., 21: 213–222.
- FORSTER, R. & SCHOLZ, G., (1979): *Salaziceras nigerianum* n. sp. from south-east Nigeria: Faunal evidence for an open seaway between the northern and southern Atlantic in Late Albian times. – N. Jb. Geol. Paläont. Mh., 1979/2: 109–119.
- GIER, R. (1964): Die Grossfauna der Mukronatenkreide (unteres Obercampan) im östlichen Münsterland. – Fortschr. Geol. Rheinl. u. Westf., 7: 213–294.
- HALLAM, A. (1969): Faunal Realms and Facies in the Jurassic. – Palaeontology, 12: 1–18.
- (1972): Diversity and density characteristics of Pliensbachian-Toarcian mollusc and brachiopod faunas of North Atlantic margins. – Lethaia, 5: 389–412.
- HANCOCK, J. M., KENNEDY, W. J. & KLAUMANN, H. (1972): Ammonites from the transgressive Cretaceous on the Rhenish Massif, Germany. – Palaeontology, 15: 445–449.
- & KENNEDY, W. J. (1981): Upper Cretaceous ammonite stratigraphy: some current problems. – In: HOUSE, M. R. & SENIOR, J. R. (Eds.): The Ammonoidea, Systematic Assoc. Spec. Vol., 18: 531–553.
- HOWARTH, M. K. (1960): Cretaceous ammonites and nautiloids from Angola. – Bull. Br. Mus. Nat. Hist. (Geol.), 10: 337–412.
- IMMEL, H., KLINGER, H. & WIEDMANN, J. (1982): Die Cephalopoden des Unteren Santon der Gosau von Brandenburg/Tirol, Österreich. – Zitteliana, 8: 3–32.
- J.E.C.O.L.N. (1980): *Nautilus macromphalus* in captivity. – Tokai University Press.
- JUIGNET, P. & KENNEDY, W. J. (1976): Faunes d'Ammonites et biostratigraphie comparée du Cénomanien du nord-ouest de la France (Normandie) et du sud de l'Angleterre. – Bull. Trimestriel Soc. Géol. Normandie etc., 63/2: 1–193.
- KATZ, H. R. (1963): Revision of Cretaceous stratigraphy in Patagonian Cordillera of Ultima Esperanza, Magallanes Province, Chile. – Bull. Am. Ass. Petrol. Geol., 47: 506–524.
- KENNEDY, W. J. & KLINGER, H. C. (1975): Cretaceous faunas from Zululand and Natal, South Africa. Introduction, Stratigraphy. – Bull. Br. Mus. Nat. Hist. (Geol.), 25: 265–315.
- & COBBAN, W. A. (1976): Aspects of Ammonite Biology, Biogeography and Biostratigraphy. – Spec. Pap. Palaeontology, 17: 1–94.
- KLINGER, H. C. (1976): Cretaceous Heteromorph Ammonites from Zululand. – Geol. Surv. S. Afr. Mem., 69: 1–142.
- & KENNEDY, W. J. (1980): Cretaceous faunas from Zululand and Natal, South Africa. The ammonite subfamily Texanitinae Collignon, 1948. – Ann. S. Afr. Mus., 80: 1–357.
- & KENNEDY, W. J. (in prep.): Cretaceous faunas from Zululand and Natal, South Africa. The ammonite subfamily Peroniceratinae. – Ann. S. Afr. Mus.
- LOMMERZHEIM, A. (1976): Zur Palaeontologie, Fazies, Palaeogeographie und Stratigraphie der turonen Grünsande (Oberkreide) im Raum Mülheim/Broich/Speldorf (Westfalen) mit einer Beschreibung der Cephalopodenfauna. – Decheniana, 129: 197–244.
- MATSUMOTO, T. (1959): Upper Cretaceous Ammonites of California. 1. – Mem. Fac. Sci., Kyushu Univ. (D), 7: 91–171.
- (1973): Late Cretaceous Ammonoidea. – In: HALLAM, A. (Ed.): Atlas of Palaeobiogeography: 421–429. Amsterdam & New York (Elsevier).
- OWEN, H. G. (1971): Middle Albian Stratigraphy in the Anglo-Paris Basin. – Bull. Br. Mus. Nat. Hist. (Geol.) Suppl., 8: 1–164.
- (1973): Ammonite faunal provinces in the Middle and Upper Albian and their palaeogeographical significance. – In: CASEY, R. & RAWSON, P. F. (Eds.): The Boreal Lower Cretaceous: 145–154; Liverpool.
- SASTRY, M. V. A., RAO, B. R. J. & MAMGAIN, V. D. (1968): Biostratigraphic zonation of the Upper Cretaceous formations of Trichinopoly district, south India. – J. Geol. Soc. India, 2: 10–17.
- SCHLUTER, C. (1867): Beitrag zur Kenntnis der jüngsten Ammonoiten Norddeutschlands: 36 pp., Bonn (P. Henry).
- (1871–76): Die Cephalopoden der oberen deutschen Kreide. – Palaeontographica, 21: 1–24 (1871); 21: 25–120 (1872); 24: 121–264 (1876).
- STEVENS, G. R. (1973): Cretaceous Belemnites. – In: HALLAM, A. (Ed.): Atlas of Palaeobiogeography: 385–401. Amsterdam & New York (Elsevier).
- SUMMESBERGER, H. (1979): Eine obersanton Ammonitenfauna aus dem Becken von Gosau (Oberösterreich). – Ann. Naturhistor. Mus. Wien, 82: 109–176.
- WIEDMANN, J. (1973): The Albian and Cenomanian Tetragonitidae (Cretaceous Ammonoidea), with Special Reference to the Circum-Indic Species. – Eclog. Geol. Helv., 66/3: 585–616.
- , BUTT, A. & EINSELE, G. (1978): Vergleich von marokkanischen Kreide-Küstenaufschlüssen und Tiefseebohrungen (DSDP): Stratigraphie, Paläoenvironment und Subsidenz an einem passiven Kontinentalrand. – Geol. Rundschau, 67: 454–508.
- (1979): Die Ammoniten der NW-deutschen, Regensburg- und Ostalpinen Oberkreide im Vergleich mit den Oberkreidefaunen des westlichen Mediterraengebiets. – In: WIEDMANN, J. (Ed.), Aspekte der Kreide Europas, I.U.G.S. Ser. A, 6: 335–350.
- (Ed.): (1979): Aspekte der Kreide Europas. – I.U.G.S. Ser. A, 6: 680 pp.
- & SCHNEIDER, H. L. (1979): Cephalopoden und Alter der Cenoman-Transgression von Mülheim-Broich, SW-Westfalen. – In: WIEDMANN, J. (Ed.): Aspekte der Kreide Europas, I.U.G.S. Series A, 6: 645–680.
- WRIGHT, C. W. (1979): The ammonites of the English Chalk Rock (Upper Turonian). – Bull. Br. Mus. Nat. Hist. (Geol.), 31: 281–332.